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Research report

Locomotion and head scanning initiated by hypothalamic stimulation are inversely related

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Abstract

Stimulation in the hypothalamus elicits locomotor stepping. Before stepping is initiated, head scanning movements occur. We determined the relationships between the latency of locomotor initiation and the number, extent and direction of the head scanning movements. Chronic stimulation electrodes were stereotaxically implanted in and around the hypothalamus of 29 rats. Under awake conditions, 38 locomotor sites were tested in a runway apparatus. Behaviors occurring between the onset of stimulation and the first step were recorded on videotape. Points on the rat were digitized at sampling rate of 6 Hz to produce measures of head angles in the vertical, horizontal, and sagittal planes. The priming paradigm was used with a current selected for each site that was minimally sufficient to produce reliable stepping. In trials at approximately 1-min intervals, a 5-s train of stimulation (the control) was followed by a second train (the test) delivered 5–20 s later. Initiation latency on control trains was strongly correlated with head movement measures. Vertical and lateral head movements were independent of one another. Together, their frequency and extent accounted for 85% of the variance in locomotor initiation latencies. In effective priming trials, when locomotor initiation latencies were reduced on the test train, the frequency and extent of vertical and lateral head movements were also reduced. In non-effective priming trials, when latencies were not reduced, head movements were not reduced. Head scanning and locomotor initiation reflect reciprocal processes. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Locomotion; Head movements; Hypothalamus; Orienting behavior; Initiation

1. Introduction

Electrical stimulation of the hypothalamus initiates locomotor stepping in anesthetized and awake rats. With moderate current levels in the anesthetized preparation, there is a latent period of approximately 3 s in which rapid respiratory and vibrissae movements appear and one or both of the hindlimbs flex. A stepping bout begins usually with a discrete extension of one hindlimb and it continues for the duration of the stimulation train [22]. In the awake rat, stimulation in the hypothalamus elicits locomotion at latencies similar to those in the anesthetized condition [24], but the latent period is seen to be occupied by head scanning movements [4,17,25]. These head movements appear to be part of the orienting/investigating repertoire performed by the rat to sample its proximal space. The head scanning phase is terminated with the appearance of a prelocomotor synergy expressed in a loosely coordinated movement of the hindlimbs and neck [23]. The head orients to the sagittal plane, the vertical head

Abbreviations: DM, dorsomedial nucleus; F, fornix; LH, lateral hypothalamus; MM, medial mammillary nucleus; mt, mammillothalamic tract; PeF, perifornical nucleus; PH, posterior hypothalamic nucleus; SuM, supramammillary nucleus; VM, ventromedial nucleus; ZI, zona incerta.

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angle lowers, and the hindlimbs and neck extend to move the center of mass forward. The onset of locomotion is marked by a liftoff of one of the forepaws. In summary, following the onset of hypothalamic locomotor stimulation in the awake rat, a sequence of motor events leads to the initiation of locomotion: head scanning, the prelocomotor hindlimb/neck synergy, and finally, forepaw liftoff.

There appears to be a reciprocal, and possibly antagonistic, relationship between the head scanning and the locomotor phases. Lateral and vertical scanning head movements are made with an orientation of the cervical spine which is more vertical than that occurring during locomotion [5,15,23]. During the head scanning phase the hindquarters of the rat remain immobile. The prelocomotor hindlimb/neck synergy then appears abruptly prior to the first step. This pattern suggests that postural stability is achieved during head scanning movements by fixing the hindquarters and suppressing the prelocomotor hindlimb/neck synergy [23]. By blocking the prelocomotor synergy, scanning head movements would preclude the onset of locomotion.

If head scanning and locomotor initiation are antagonistic, then they should covary inversely. Locomotor stimulation sites in and around the hypothalamus were used to test this proposition in two ways. First, in a multivariate correlation approach, we determined if the differences in baseline initiation latencies between sites were related to head scanning differences. Specifically, the antagonism hypothesis predicted that initiation latencies would be longer at sites where stimulation produced more numerous or more extensive head movements. Conversely, sites with shorter locomotor latencies should have fewer or less extensive head movements. Second, we facilitated locomotor initiation by means of the priming paradigm to test the effect on head scanning. The priming effect is the facilitation of locomotor initiation that is seen on the second of two closely presented stimulation trains. It has been demonstrated in the anesthetized rat [29]. Priming of locomotor initiation has not yet been demonstrated in the awake rat with hypothalamic stimulation, although a similar phenomenon has been demonstrated in the context of intracranial self stimulation [13]. If head scanning is antagonistic to locomotor initiation, then the reduction of initiation latencies should be accompanied by a reduction in the frequency or extent of head movements. Alternatively, head scanning might not be antagonistic to locomotor initiation. Rather, they might be components of a single sequential process that is facilitated during the priming effect. In this case, the reduced locomotor latencies should be accompanied by faster, but no less extensive, head scanning. In contrast, the antagonism hypothesis specifically predicts that head scans should be reduced in extent or number when locomotor initiation is facilitated in the priming paradigm.

2. Methods

2.1. Subjects

The subjects were 29 male Sprague–Dawley rats bred from stock obtained from the Charles River Company. They weighed 272–507 g at surgery. The rats were housed singly under a reversed light cycle (12/12 h); they were tested during the dark period.

2.2. Surgery

Implantation of chronic stimulation electrodes was performed under Nembutal anesthesia (40–50 mg/kg), injected intraperitoneally, with supplemental Nembutal (10 mg/kg) given as needed during the surgery. The rats were mounted in a stereotaxic apparatus with the head adjusted so that Bregma and Lambda were on the horizontal plane. Holes were drilled in the skull to receive anchoring screws and stimulation electrodes. Stimulation electrodes were monopolar 125-μm diameter stainless steel wires insulated with Teflon, except at the cross-section of the tip. A bare wire was wrapped around six screws in the skull to serve as the return line for the stimulation circuit. The electrodes and return wire terminated in Amphenol pins which were inserted in a plastic connector strip that was secured to the skull screws with dental acrylic. Antibiotic ointment was applied to the incision and the rat recovered for at least 5 days before testing.

2.3. Apparatus

The rats were tested in a runway/treadmill constructed of clear acrylic (77 cm long, 12 cm wide, 39 cm high). A treadmill belt on the floor of the runway moved in a rearward direction when infrared sensors mounted detected the rat's absence from a starting position located at the midsection of the runway. The belt was also activated by the tester whenever the rat was facing to the rear. The maximum belt speed used was 13.3 cm/s. The rats could easily match this speed, but they eventually learned to sit or stand at the starting position facing the front. Two video cameras were focused on the starting position to allow measurement of head and neck movements. One mounted 46 cm from the wall of the runway provided a 32×14 cm side view and showed vertical movements and neck extensions. Another camera mounted 133 cm above the base of the runway provided a 15×10 cm superior view and showed lateral head movements. The two camera signals were combined and recorded along with a time-marker. A flexible cable connected to the strip on the rat's head allowed the stimulation of the hypothalamic locomotor electrodes. The stimulation train was 5 s in duration, and composed of constant-current

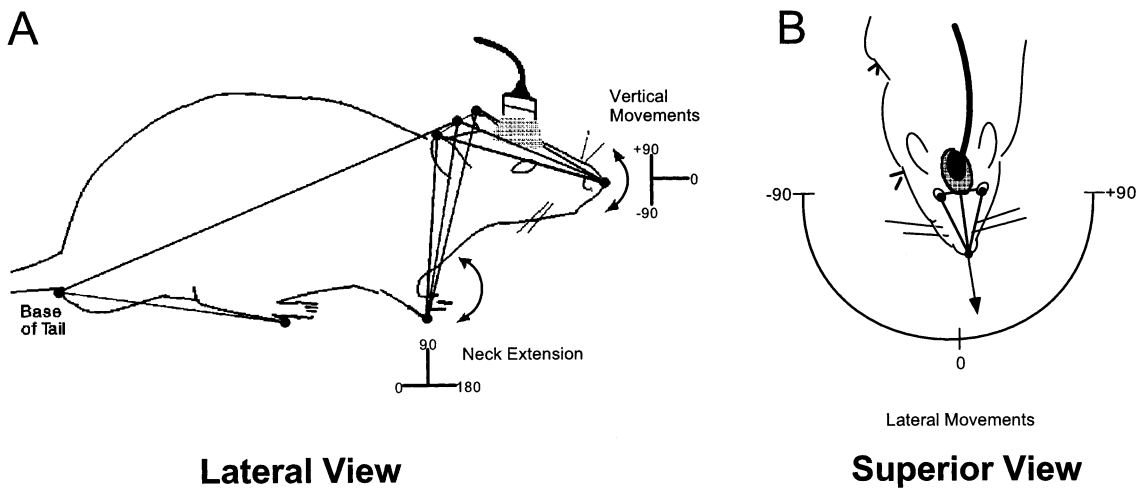


Fig. 1. Schematic illustration of the digitizing method used to measure head movements. (A) The lateral view camera showed seven points on the rat which were connected by segments. Vertical head movements were indexed by changes in the angle relative to horizontal of the segment from the nose to the mid-pinnae point. Neck extension was indexed by the angle relative to the horizontal of the segment from the right forepaw to the mid-pinnae point. (B) The superior view camera showed three points (eyes and nose). Lateral head movements were indexed by the changes in the angle of the segment from the nose to the mid-eye point relative to the side of the runway.

biphasic pulses (each phase 0.5 ms duration) at 50 Hz. At the onset of stimulation, a marker superimposed on the video image marked the start of the control or test stimulation trains.

2.4. Testing procedure

In two preliminary sessions, the hypothalamic sites were screened for locomotor effects by testing a range of currents up to 100 μA. Sites that were negative were not tested further. Sites at which stimulation reliably elicited forward locomotion with minimal competing body turns, rearing, or belt-biting were tested further in a videotaping session.

The objectives of the test session were to select a current which elicited reliable stepping with a latency of 3–5 s, and to record approximately 20 complete trials. In a complete trial, an initial train of stimulation (control) was followed in approximately 10 s by a another train of stimulation (test). A 10-s control-test interval was optimal to allow the locomotor response of the control stimulation to decline, and to produce a reduction in the locomotor initiation latency on the test train (the priming effect). Approximately 60 s elapsed between the offset of a test train and the onset of the subsequent control train.

In order to present either the control or test train, it was necessary that the rat be in view of the cameras, with its head oriented to the front of the runway, and remain relatively still for at least 1 s. After the rat walked during the control train, it was returned to the starting position by the rearward movement of the belt. The rat could delay the start of the test train if it continued walking counter to the belt movement, or if it was not oriented properly, or engaged in grooming or head movements at the starting position. If the delay exceeded approximately 20 s, the trial was aborted, and another trial was attempted after 40 s. Trials were also aborted if any of the following events occurred during the control train: failure to initiate stepping within 5 s, rearing or body turns which lifted a forepaw off the floor, moving the head out of camera field, biting the belt, and extreme lateral or vertical head angles at the start of stimulation. If any of these events occurred on the test phase of the trial, the trial was unusable for motion analysis. About 60 min was required to test one site; if a rat had two locomotor sites, both were tested in the same session. Current was adjusted as needed to maintain reliable stepping during the control train at a latency of 3–5 s. Some rats required a second session to yield a sufficient number of usable trials.

2.5. Motion analysis

From the 20 tentatively usable trials in the test session, at least five trials were expected to be appropriate for head movement measurement. This expectation was met for most of the sites (see Section 3). Trials were lost to the motion analysis for the reasons listed above, and if the liftoff of the forepaw which initiated stepping could not be determined with certainty, or if the initiation latency during the control stimulation was 1 s or less which made a priming effect difficult to detect. The videotape records were digitized (Peak Performance) at a sampling rate of 6 Hz. For each trial, sampling began at the first frame showing the onset of stimulation and continued up to, but did not include, the frame at which the liftoff of first step occurred.

The points on the rat that were digitized are illustrated in Fig. 1. The points digitized from the lateral view were: the nose, superior aspects of the right and left pinnae, the midpoint of the inter-pinnae line, the distal end of the lateral digit of the right forepaw, the distal end of the lateral digit of the right hindpaw, and the base of the tail. The points digitized from the superior view were: the nose, each eye, and midpoint between the eyes. In addition, two points on the runway wall were digitized to provide a reference for angle calculation.

Three elemental measures were derived from these points using the Peak Performance algorithms. Vertical head position was indexed as the angle of the segment from the nose to midear, relative to objective horizontal. Neck extension was indexed by the angle of the segment from the forepaw to the midear, relative to objective horizontal. Position of the head in the horizontal plane was indexed as the angle of the segment from mid-eye to the nose, relative to the wall of the runway.

From the three elemental measures, several head position and movement variables were computed for each stimulation train by customized programs. The first two groups of measures were static. Initial values of vertical and lateral head position and neck extension were taken from the first sample at the start of stimulation. Final values were taken from the sample preceding the liftoff of the first limb to step. The remaining two classes of measures were dynamic and non-directional. Frequency of movement was separately measured for vertical and lateral head movements and neck extensions. It indexed the number of discrete head movements in the time from the start of stimulation to the first step. A discrete movement was declared when an angle reversed direction, or when it changed more than 1° after one sample period with no change. The principal measure of the extent of head movement was provided by the range in each of the dimensions. It was defined as the difference between the minimum and maximum values. Finally, the following measures of vertical and lateral movements were dynamic and directionally specific. These directional integrals were summations which provided a measure for each sub-dimension: up, down, contralateral and ipsilateral. Overall integrals which reflect the predominance of one direction were also determined for vertical and lateral movements.

2.6. Histology

When testing was completed, the rats were given a lethal dose of Nembutal and perfused through the heart with 0.9% saline followed by 10% formalin. Following further fixation, the brain was sectioned transversely at 100 μm with a vibratome. The sections were viewed with a dissecting microscope. The locations of the stimulation sites were plotted onto atlas drawings [20].

3. Results

3.1. Overview of head movements and locomotor initiation on the control trains

The locations of the 38 stimulation sites are illustrated in Fig. 2. The sites ranged on the anteroposterior dimension of the hypothalamus from the level of the

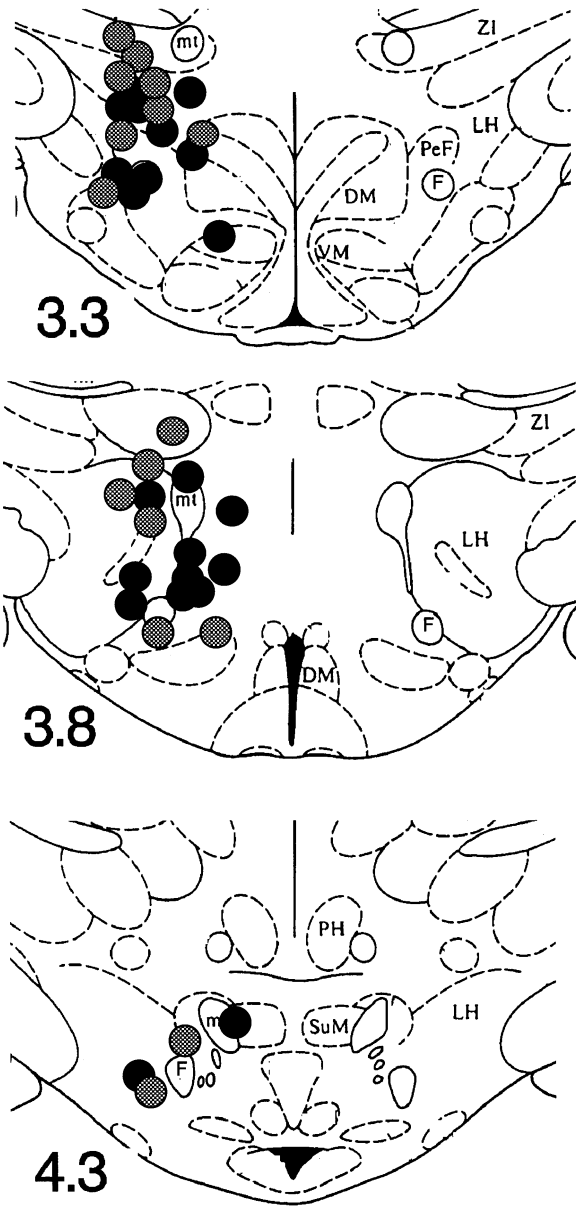


Fig. 2. Schematic illustration of the locations of the stimulation sites in and around the hypothalamus. The gray symbols represent sites used in the analysis of the relations between the priming effect and head movements. Drawings adapted from the atlas of Paxinos and Watson [20]. Numbers indicate mm posterior to Bregma.

dorsomedial nucleus (DM) to the posterior nucleus (PH). On the mediolateral dimension, the sites ranged from the medial nuclei (DM, PH) to the lateral hypothalamus (LH) with the fornix (F) and the mammillothalamic tract (mt) forming the approximate center of the distribution. On the dorsoventral dimension, the sites ranged from the ventral LH to the zona incerta (ZI). The mean of each of the variables over trials was used to characterize a site. Most of the sites (21/38) had five or more usable trials; four sites had two trials and four sites had nine or more trials.

The current for each site was selected with the intention of producing initiation latencies during the control stimulation train that were more than 3 s. Such long latencies facilitate the detection of priming effects during the test train. The currents used averaged 38.9 μA (SEM ± 2.7). Overall, the control latencies that were achieved were on the low side of the objective; the mean latency for the 38 sites was 3.02 s (± 0.12).

For the control trains, locomotor stimulation at the 38 sites produced a mean frequency of 6.3 (± 0.27) lateral and 7.0 (± 0.29) vertical head movements. Vertical movements were more frequent than lateral movements ($t(37) = 2.30$, $p < 0.01$). Downward movements were more extensive (larger directional integral) than upward movements ($t(37) = 5.70$, $p < 0.01$), and contralateral movements were more extensive than ipsilateral ($t(37) = 2.15$, $p < 0.05$). At some sites, the initial vertical movement was consistently up ($N = 3$) or down ($N = 5$), but at most sites the initial movement varied. Similar variability appeared in the initial lateral movement; eight sites were consistently ipsilateral, seven were consistently contralateral, but the majority were inconsistent. Almost all stepping began with the liftoff of a forelimb, the laterality of which did not correlate with the overall head movement pattern in any direction. For ten sites, the first limb to step was consistent: ipsilateral ($N = 5$) or contralateral ($N = 5$) to the site of stimulation. For the remaining 28 sites, the laterality of first step varied across trials.

3.2. Correlation between control head movements and locomotor initiation multivariate analyses

As a first step, a principal-components analysis was performed to determine whether there was redundancy in the various head movement measures. The dynamic and directionally specific head movement variables were used: frequencies of vertical and lateral movements, and integrals of upward, downward, ipsilateral, and contralateral movements. The first component, which we term general head movement, accounted for 38% of the total variance. Frequencies of both vertical and lateral movements, and integrals of upward and ipsilateral movements all had positive loadings with it. The second component, termed ipsilateral movement, accounted for 21% of the total variance; the contralateral integral loaded negatively and the ipsilateral integral loaded positively with it. The third component, upward movement, accounted for 19% of the variance. Together, these three components accounted for 79% of the variance. Current level did not correlate with any of the components. This analysis indicated that vertical and lateral movements both contribute to a general head movement factor but movements on one dimension were independent of movements on the other.

A step-wise linear regression analysis was used to assess the dependency of locomotor initiation on head movements. Four measures accounted for 85% of the variance in initiation latencies between sites. The head movement measures were: vertical and lateral frequencies, upward integral, and lateral range. The regression equation and the relationship of actual latencies to the fitted line are shown in Fig. 3.

3.3. Anatomical correlations with head movement patterns

The extent of contralateral head movements was greater than the extent of ipsilateral movements. Aside from this non-surprising relationship, head movement patterns showed no apparent dependence on the location of the site of stimulation. Head movement patterns elicited at a given site were generally consistent across trials. However, a similarly located site in another rat could have an equally reliable but different pattern. The anatomical parameters that were examined included mediolateral and dorsoventral coordinates, proximity to the fornix, and regional location (e.g. zona incerta, perifornical nucleus, lateral hypothalamus).

3.4. The priming effect and head movements

This analysis tested the prediction that directly reducing the initiation latencies would reduce the extent or number of head movements. It used a subset ($N = 16$) of the survey sites which are indicated in Fig. 2 as gray symbols. In testing these sites, the goal was to present a test train within 20 s of the termination of a control train. Of the trials used ($N = 97$), all had control-test intervals of 21 s or less. Priming effects (defined as a reduction > 0.5 s in latency on a test) were produced on most (66/97), but not all, trials. Most sites (10/16) had both trials in which priming was effective and non-effective. Four sites had trials with only priming effects, while two sites had trials with no priming effects. Although not in the original design of the study, the comparison of head movements on trials with no priming effects provided a useful means of further testing the relationship between locomotor initiation and head movements.

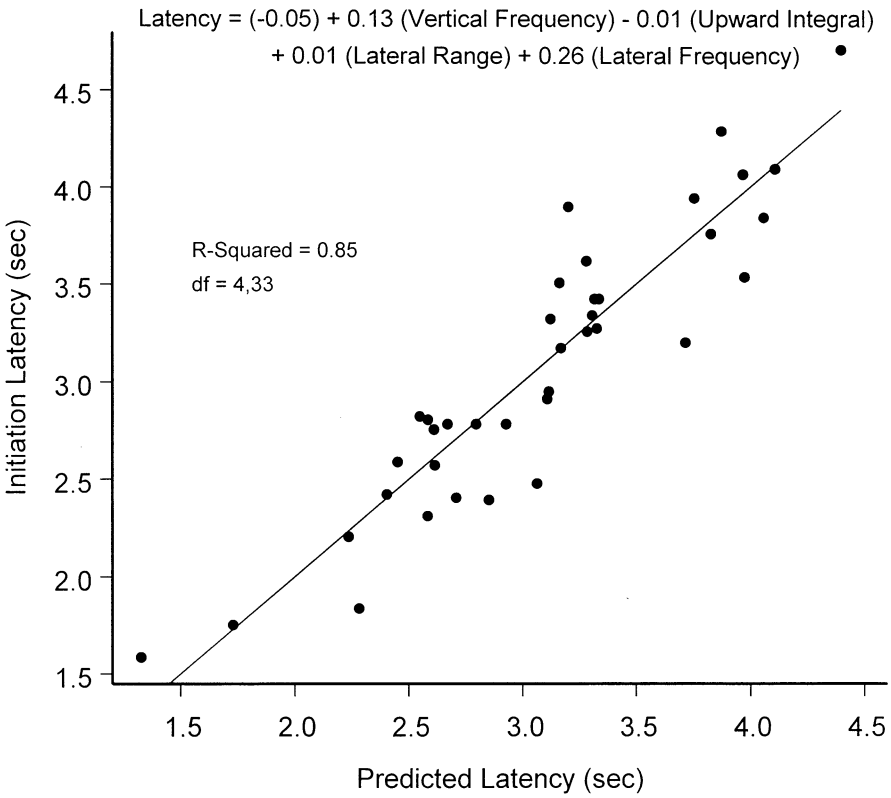


Fig. 3. The dependence of locomotor initiation latency on head movements. Inter-site ($N = 38$) variance in mean initiation latencies on the control trains is substantially accounted for (85%) by two vertical head movement measures (frequency and upward integral) and two lateral head movement measures (frequency and range).

In trials exhibiting priming effects, head movements were consistently reduced during the test trains. The main findings are shown on the left side of Fig. 4. The priming effect itself is shown in Fig. 4(A). The locomotor latencies during the control train averaged 3.38 s (± 0.18), and the latencies during the test train averaged 1.91 s (± 0.19). On the test train, the rat made fewer vertical head movements ($t(13) = 5.83$, $p < 0.01$), and they had a reduced range ($t(13) = 4.88$, $p < 0.01$). These differences are shown in Fig. 4(B), left. Fewer lateral head movements also appeared on the test train ($t(13) = 7.52$, $p < 0.01$), and they too were less extensive in range ($t(13) = 4.83$, $p < 0.01$). These differences are shown in Fig. 4(C), left. At the onset of the test train, the rat's posture more closely matched the posture that has been found to precede the first step [23]. Specifically, the vertical head angle was 6.58° lower ($t(13) = 2.47$, $p < 0.01$) and neck extension angle was 3.36° greater ($t(13) = 2.67$, $p < 0.01$) at the onset of the test train compared to the onset of the control train. On the sample just before the first step, the vertical head and neck extension angles on the control and test trains did not differ.

If the reductions in head movements are specifically related to the facilitation of locomotion, then they should not occur when priming fails to occur. As shown on the right side of Fig. 4, head movements were not reduced on the 31 trials in which priming effects were absent. No differences between the control and test trains for any of the head movement variables were found for these trials. One factor responsible for the absence of priming on these trials was their longer control-test intervals. The trials with priming effects had a mean control-test interval of 9.89 s (± 0.94), whereas in contrast, the trials with no priming effects had a control-test interval of 12.81 s (± 1.16). This difference was small but reliable ($t(9) = 3.20$, $p < 0.02$). The interval was partially determined by the rat's post control behavior (see Section 2.4). However, the control-test interval may not have been the only factor. Fig. 4(A) shows that the control latencies were low on the trials with no priming effects ($t(9) = 2.73$, $p < 0.05$), and the initial low levels may have impeded further reductions in latency on these trials. Although the reason for a lack of priming effects is not clear, the important feature is that trials without reductions in initiation latencies also showed no reductions in head movements. Regardless of the reason for the lack of priming effects during these test trains, the absence of reductions in both initiation latency and head movement during these trains is significant. The pattern is consistent with the previous demonstration that prim-

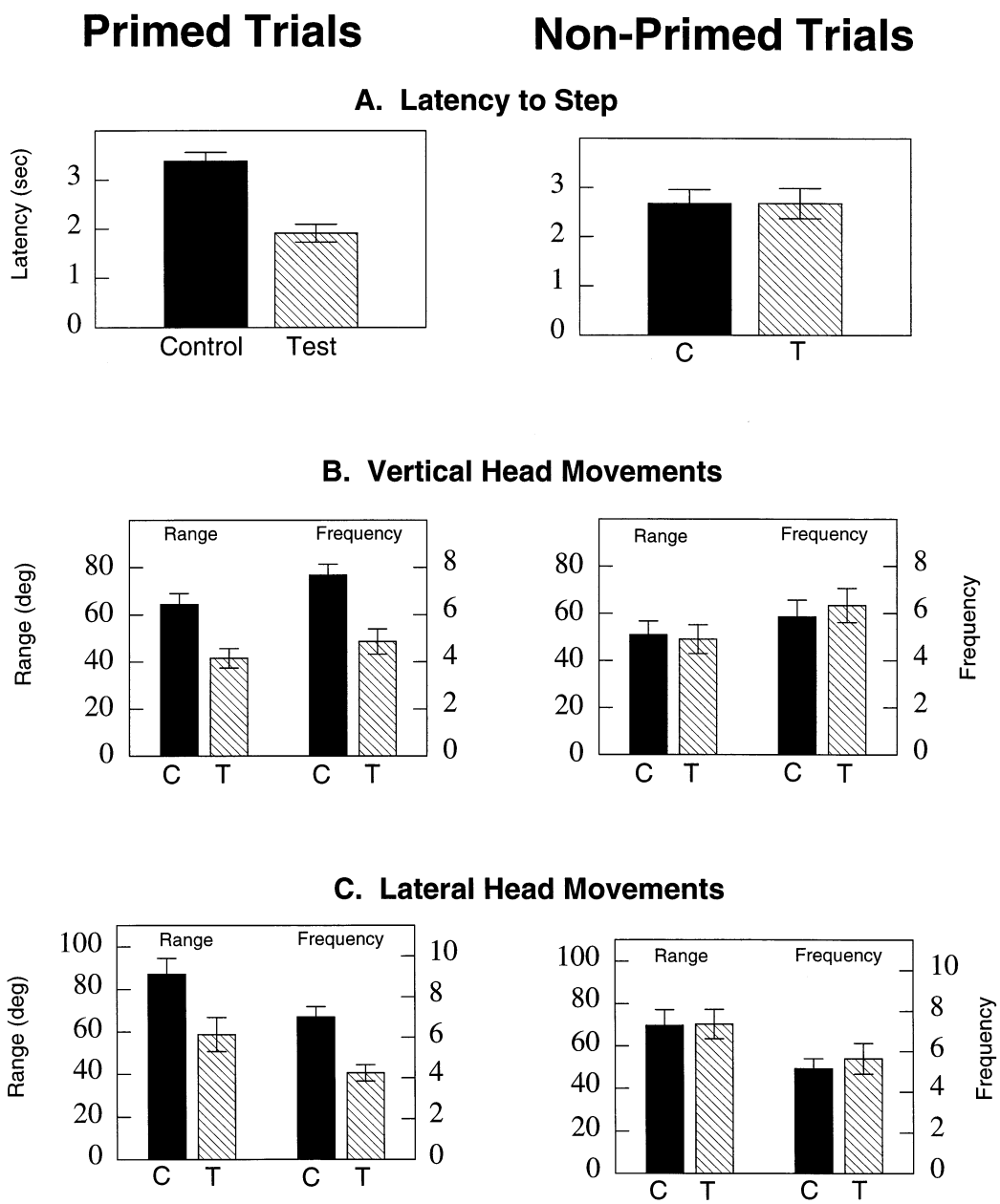


Fig. 4. Comparison of various measures between control and test trains. Left side shows means for 66 trials (14 sites) which showed a priming effect. Right side shows means for 31 trials (12 sites) which did not show a priming effect. (A) Latency to initiate stepping. (B) Range and frequency of vertical head movements. (C) Range and frequency of lateral head movements.

ing effects are associated with reductions in both initiation latency and head movement.

Fig. 5 illustrates a representative trial in which head movements were decreased when the priming procedure effectively reduced the locomotor latency on a test train. The latency to step was 4.51 s during the control train and 2.84 s during the test. Each of the four panels shows two stick figures: one at the onset of the stimulation (the triangular head is filled), and one just before the first step (the triangular head is stippled). During the control train (left side), the rat showed the characteristic lowered head angle and increased neck extension prior to the first step. The irregular line traces the trajectory of the nose from the onset of stimulation to the first step. The vertical head movements are shown in the lateral view (upper left panel); in this case, the rat made an initial series of upward movements which were followed by a series of upward and downward movements. The lateral head movements are shown in the superior view (lower left panel); here the rat started with a right movement (contralateral); it was followed by a left movement, a centering movement to the right, and finally stepping commenced with the head oriented to the right. Behavior during the test train illustrated on

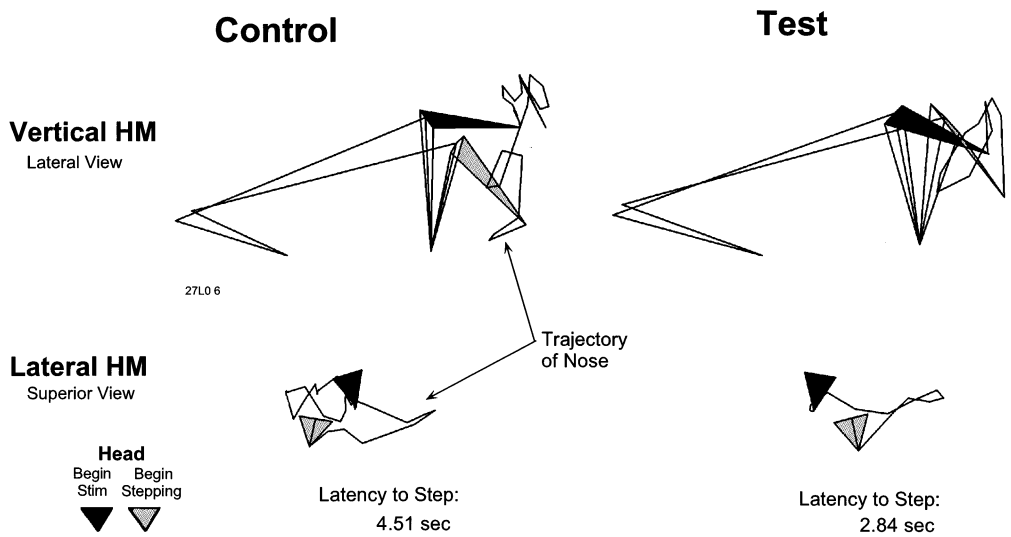


Fig. 5. Stick figures from a representative trial showing a priming effect. The reduced latency of stepping during the test trial is associated with a reduction in the overall extent of both vertical and lateral head movements.

the right side. Accompanying the shorter initiation latency were reductions in both vertical and lateral head movements.

4. Discussion

These results provide converging evidence that the head scanning movements and locomotor stepping elicited by hypothalamic stimulation reflect reciprocal processes. First, the variation in baseline locomotor latencies was largely explained by head movements. The strength of this relationship was unexpected because currents were selected with the intention of producing similar control latencies for each site. In so far as this procedure was effective in reducing the range of latencies, it would have minimized any correlation. The present analysis may therefore provide a conservative estimate of the relationship between head scanning and locomotor initiation. Second, a direct manipulation of locomotor initiation latency by means of the priming paradigm showed that faster initiation of stepping was preceded by fewer and less extensive head movements. The possibility that faster stepping initiation was associated with the same head movement pattern merely performed faster was shown not to be the case. Both the quantitative and stick-figure analyses showed that the head movement patterns during the test train were reduced in frequency and extent compared to the control. Third, on trials when the priming paradigm was not effective in making locomotor initiation faster, it also did not reduce head movements. In general, the consistency and magnitude of these relationships indicate that head scanning reflects a fundamentally important process interacting with locomotor initiation.

Two behavioral patterns can be difficult to execute simultaneously because they require forces to be applied to the same effector in different ways. Incompatibilities of this type would lead indexes of these patterns to be inversely related, but that alone would not imply that their neural control systems were reciprocally related. Therefore, it is reasonable to entertain the possibility that the hypothalamic stimulation might have nonspecifically activated two independent motor systems (head scanning and locomotion) which were to some extent kinetically incompatible. By this interpretation, the inverse relationship between the measures of head scanning and locomotor initiation observed here then would reflect this interference rather than an antagonism between the neural control circuits. If the present observations documented only the inverse relation between scanning and stepping in the baseline condition, then the incompatibility interpretation would be both parsimonious and persuasive. However, it was also found that facilitated stepping in the priming paradigm stepping came at the expense of head scanning. If scanning and stepping were simply independently elicited but conflicting behavioral patterns, there would be no reason to expect priming effects to differ for them. However, it was found that priming stimulation facilitated stepping while it reduced head scanning. Given this divergence, the findings indicate that head scanning and locomotor initiation are not just two conflicting but otherwise independent behavior patterns elicited by hypothalamic stimulation, but rather they are reciprocally related.

The reciprocity of locomotor initiation and head scanning found here extends earlier studies of locomotion elicited by stimulation of the hypothalamus. The elicited pattern has been described in general terms as

exploratory or investigatory locomotion as it is accompanied by head scans and sniffing [1,4,10,17,18,25]. The reciprocity found here as well as descriptions of natural and apomorphine-elicited exploration in the rat [8,14,27,28] suggests that a finer grain analysis would have found the elicited exploratory behavior to be deconstructed into alternating bouts of locomotion and head scanning. It is possible to describe in specific terms the morphology of the exploratory locomotion that would be expected from stimulation of the hypothalamus. The locomotor bouts would be characterized by low vertical head angles that permit contact of the vibrissae and snout on the substrate, and maintenance of the head near the sagittal plane. Although the head would be generally centered, small amplitude head scans would occur in which the rat maintains a 'loose sliding snout contact' with the substrate [27]. The head scanning episodes would be characterized by a cessation of forward progression by arrest of the hindlimbs, and larger displacement head movements in both the lateral and vertical planes. Deviations from this prototypic pattern by the actual pattern of exploratory locomotion elicited by hypothalamic stimulation could reveal new regional and behavioral subsystems.

The variability and lack of regional differences in the head movement patterns were unexpected. Although there was gross similarity in the pattern for a given site, the specific sequences of movements were not consistent from trial to trial. The location of the stimulation site determined only the overall contralateral dominance of head movement sequences. Low current levels may have contributed to the variability, but a major factor probably was the exclusion of sites at which stimulation produced strong head movements. These sites were excluded because the associated body turns or rearing competed with locomotor initiation. The variable pattern of head movements seen here suggests that the stimulation activated diffuse and non-topographic projections to head movement control circuitry. The variability of head movement patterns for a given site would contribute to the lack of regional correlations. Based on previous experiments that contrasted aversive and appetitive locomotor sites, we had expected to differentiate medial and lateral sites on the basis of vertical head movements [7,18,19]. Low currents should have aided in localization, but the activation of fibers of passage remains a problem for mapping studies using electrical stimulation. Chemical injections may provide a better approach to regional differences in head movements.

The reciprocity of head scanning and locomotion that was found here was required by the hypothesis that there is a mutual antagonism between locomotor initiation and head scanning systems. However, the present findings do not prove the hypothesis. Consideration of the basis for the reciprocity bears on the more general issue of the roles of these behavior patterns in exploration, foraging and patrol. There is a well developed body of evidence based on lesion, pharmacological, and developmental studies in the rat showing that lateral head scanning and locomotion are separate subsystems of exploration [28]. During normal development of mobility [8], as well as during recovery from hypothalamic lesions [14], there is a succession in the exploratory patterns from immobility, to lateral head scanning with the hindquarters fixed, to pivoting with one hindlimb stepping, to forward progression with alternating hindlimb stepping. In normal adult rats, systemic injection of apomorphine produces a generally similar but exaggerated pattern that is reversed in sequence [27]. Consistent with these findings, trade-offs between the effects on locomotion and stereotypic head movements have been frequently found in studies of amphetamine [21,26], and lesions in the tectum [11] and median raphe [31]. These findings make it clear that head scanning and locomotion, though part of the same general system of exploration, occur at different times and are differentially affected by lesions and drugs.

Additional evidence indicates that head scanning appears in normal adults when there is a transition from immobility to locomotion. Rats in a semi-natural burrow system respond to the threat of a potential predator by showing increased immobility at the exit of the burrow and engaging in prolonged lateral head scanning prior to locomotion into an open field [2]. In the radial arm maze, normal rats, but not rats with lesions of the superior colliculus, pause in the central region to make head scans before locomotion to the chosen arm [6]. After rats complete eating in a posture characterized by immobile hindquarters, they engage in lateral head scanning which culminates in forward progression. The post-prandial head scanning does not appear to be directed to food retrieval, but its duration does correlate with the amount of time spent in the immobile posture [30]. In the present study, both the control and test stimulation were applied when the rat was immobile, but the priming paradigm required that the control-test interval be brief, and therefore the period of prior immobility was shorter when the test stimulation was presented. Thus the reduced head scanning and shorter locomotor latency on the test was associated with less prior immobility.

If the transition from immobility to locomotion is associated with increased head scanning, it raises the possibility that head scanning could both antagonize locomotion and enable it. In this interpretation, head scanning would provide a bridge to locomotion that would be come into play when suppressive processes were dominant, as in the case of threat or the need to stop and scan for information. In cases of weak suppression, as when locomotion had been recently activated or when threat became attack, locomotor

initiation would dominate and head scanning would not appear. This proposed role of head scanning is consistent with the warm-up phenomenon by which rats appear to break out of prolonged immobility by engaging in head scans of progressively greater amplitude [14,30]. Applied to the present findings, this proposal suggests that increased head scanning would be associated with long locomotor initiation latencies because there was a greater degree of immobility to overcome. The interesting paradox of this proposal is while head scanning ultimately would enable locomotion by counteracting immobility, its execution would antagonize locomotion in the short term because of the demands for postural stability (see Section 1). Although this proposal opens some interesting questions, it is complex and reaches beyond the available data which seems at this time to be sufficiently explained by the idea that head scanning and locomotor are mutually antagonistic.

The head movement patterns showed variability and a lack of regional differences, properties shared by the locomotor priming effect. It is therefore reasonable to consider the degree to which priming and head movements might be directly linked. In the anesthetized rat [29], generally similar priming effects are produced at sites throughout the hypothalamus. The facilitation on the test train almost always occurs but the magnitude of the effect is variable. Priming appears to reflect widespread processes. It occurs with the control and test stimulation applied to the same site, or with the control and test stimulation applied to different sites [29]. Could a reduction in antagonistic head movements with repeated stimulation account for the facilitation of locomotion in the priming paradigm? If head scanning is refractory to repeated activation, then the priming paradigm might operate through disinhibition to facilitate locomotor initiation. Head movement circuitry is subject to tonic inhibition through striatal projections from the substantia nigra reticulata [3]. The zona incerta sends a GABA projection to tectal cells which are the origin of the predorsal bundle, and a negative feedback function has been suggested for it [16]. The anterior dorsal tegmentum of the midbrain contains neurons that are selectively active prior to the initiation of stepping in the anesthetized rat [9]. This region has been implicated in the control of vertical head and eye movements [12], and they also might function in the inhibition of head movements and the indirect facilitation of locomotion.

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